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THE SKULL OF *DISSOPSALIS CARNIFEX* PILGRIM, A MIOCENE CREODONT FROM INDIA

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The Creodonts are generally considered as typical of Eocene times, with occasional phylogenetic lines extending into the Oligocene period, when the entire suborder became virtually extinct. Discoveries made in the last score of years have shown us that two genera of creodonts, both of them belonging to the hyaenodont group, persisted into the Miocene period. One of these genera, *Metapterodon*, is from the diamond fields of South Africa, and its stratigraphic position shows that it barely survived the transition from Oligocene into Miocene times.[1] The other genus, *Dissopsalis*, from the lower Siwalik beds of northern India, persisted well into the Miocene period, and consequently is the last known survivor of creodont evolution.

Dissopsalis was described by Pilgrim on the basis of some scattered and fragmentary teeth.[2] Subsequent to the description of his original material, no new finds came to light until 1922, when Mr. Barnum Brown of the American Museum obtained a skull and part of a mandible, as well as several scattered teeth, from the lower Siwalik beds of the northern Punjab States. These remains, hitherto undescribed, form the basis of the description in this paper. Further and more critical considerations of the genus will be presented in a subsequent work, which will comprise a detailed examination of the entire Siwalik fauna in the American Museum.

The drawings in this paper are by John C. Germann and Margaret Matthew.

Order Carnivora
Suborder Creodonta
Superfamily Pseudocreodi
Family Hyaenodontidae

[1]Stromer, E. 1926. Reste Land- und Süsswasser-Bewohnender Wirbeltiere aus den Diamantfeldern Deutsch-Südwestafrikas. Sonderabdruck aus E. Kaiser, Die Diamantenwüste Südwestafrikas, Bd. II, pp. 110–112, pl. 40, figs. 13, 14.

[2]Pilgrim, G. E. 1910. Notices of New Mammalian Genera and Species from the Tertiaries of India. Rec. Geol. Surv. India, Vol. XL, Pt. 1, p. 64. (*Dissopsalis carnifex, Dissopsalis ruber.*)

Pilgrim, G. E. 1914. Description of Teeth Referable to the Lower Siwalik Creodont Genus *Dissopsalis*, Pilgrim. Rec. Geol. Surv. India, Vol. XLIV, Pt. 4, pp. 265–279, pl. 29.

Dissopsalis carnifex Pilgrim

SPECIMENS IN THE AMERICAN MUSEUM.—

Amer. Mus. 19401.—Skull, the palate and cheek dentition complete; rostrum anterior to P^1 missing; occipital portion shattered. Lower Siwaliks, 1600 feet above the level of Chinji Rest House, one mile north of Chinji Rest House, northern Punjab.

Amer. Mus. 19402.—Portion of a right maxilla, with P^3-M^3; also left P^2-^{3}. Lower Siwaliks, at base. East of Chinji Rest House.

Amer. Mus. 19403. —Mandibular fragment, with left M_{2-3}. Lower Siwaliks, 100 feet above level of Chinji Rest House; four miles west of Chinji Rest House.

Amer. Mus. 19339.—Left M^1. Lower Siwaliks, about 600 feet above the base, one mile north of Chinji Rest House.

Amer. Mus. 19348.—Right P^4. Lower Siwaliks, 1600 feet above level of Chinji Rest House; one mile north of Chinji Rest House.

Amer. Mus. 19349.—Left P^4, right M^2. Lower Siwaliks, 1600 feet above level of Chinji Rest House; one mile north of Chinji Rest House.

DIAGNOSIS.—

1. A fairly large hyaenodont, comparable in size to *Hyaenodon cruentus*.
2. Dentition: I ?, C, P 4/4, M 3/3; carnassial shear on M^2, M_3.
3. Premolars robust, with well developed cingula. P^4 with a very large internal protocone.
4. Molars trenchant. M^1 and M^2 with large protocone, appressed paracone and metacone, and with a metastyle shear. M^3 very small. Lower first and second molars with well developed trigonid and basined talonid. In M_3 the trigonid has become trenchant, while the talonid is reduced to a small tubercle.
5. Skull heavy. Frontals expanded above orbits, sagittal crest high, zygomatic arch long. Brain case constricted.
6. Palate wide, pterygoids produced posteriorly, almost reaching the glenoid articulation. Bullae presumably cartilaginous.

THE SKULL.—

The skull, Amer. Mus. 19401, was discovered by a native, who unfortunately had no knowledge of the technique of fossil collecting. Consequently he damaged the specimen irreparably while removing it from the rock, so that what had been a perfect specimen, was reduced to a muzzle, containing the cheek teeth, a fragment of the cranium, two fragments of the zygoma, and numerous small scraps too badly broken to be readily identified. Mr. Brown collected fragments and impressions of the specimen, and from this material it has been restored, thanks especially to the efforts of Mr. Otto Falkenbach, with a fair approximation to the probable appearance of the original skull. In addition to the damage done by the native collector, the skull suffered a considerable amount of crushing, due to the weight of overlying sediments, so that the maxilla was broken, while the frontals and the nasals were pushed down on the sides of the face. By making careful measurements of the

crushed parts of the maxilla, and by calculating the amount of their displacement, and in addition, by the comparison of uncrushed skulls of related animals, such as *Hyaenodon* and *Cynohyaenodon*, it has been possible to restore the skull of *Dissopsalis* to approximately its original height. (Compare fig. 1 with the restoration, fig. 4.)

As to size and general form, the skull of *Dissopsalis* is quite similar to that of *Hyaenodon cruentus*. The skull of *Dissopsalis* is broad above the orbits, from which point it decreases in width rapidly, to the front and to the back. In this genus, as in other creodonts, the brain case is restricted. The narrowest portion of the muzzle is above the second premolar, while anteriorly the rostrum becomes wider to accommodate the canines. As seen from the side, the skull is fairly high. The infra-orbital foramen is above the mid-portion of the third premolar, and as in other hyaenodonts it is situated at some distance in front of the orbit. Due to the crushing down of the frontals, the anterior border of the orbit has been slightly displaced, but the configuration of the right side of the specimen would indicate that the front of the eye socket was above the anterior border of the second molar. The nasals are long, and would appear to extend forward, as in *Hyaenodon*.

The palate is constricted between the anterior premolars, but it widens rapidly posteriorly, reaching its greatest transverse dimension between the second molars. The incisor foramina are located between the canines, and would appear to be elongated. A core of matrix indicates that the pterygoids formed either a closed tube, as in *Hyaenodon*, or a long, narrow trough, as in *Sinopa*, *Cynohyaenodon* and other early genera. This tendency for the close approximation or the joining of the pterygoid borders, causing the posterior nasal choanæ to open far to the back of the palate, was characteristic of the hyaenodont group. It probably was not connected with any aquatic habits, since otherwise the skull indicates a typically terrestrial animal, but rather was developed for a support or a protection for the pharynx. A similar development of a "pterygoid tube" may be seen in the modern procyonids, such as *Nasua*.

The rest of the skull will hardly admit a detailed description. Suffice it to say that the sagittal crest is high, a corallary of the restricted brain case and strong temporal muscles. Evidently *Dissopsalis* (and this statement is borne out by the teeth) was able to crunch the bones of fairly large animals. The glenoid fossa of the squamosal is elongated transversely, with a strong post-glenoid process and a heavy anterior border. It is relatively large, an indication that the mandibular articulation was strong. On the left side of the skull a portion of the post-

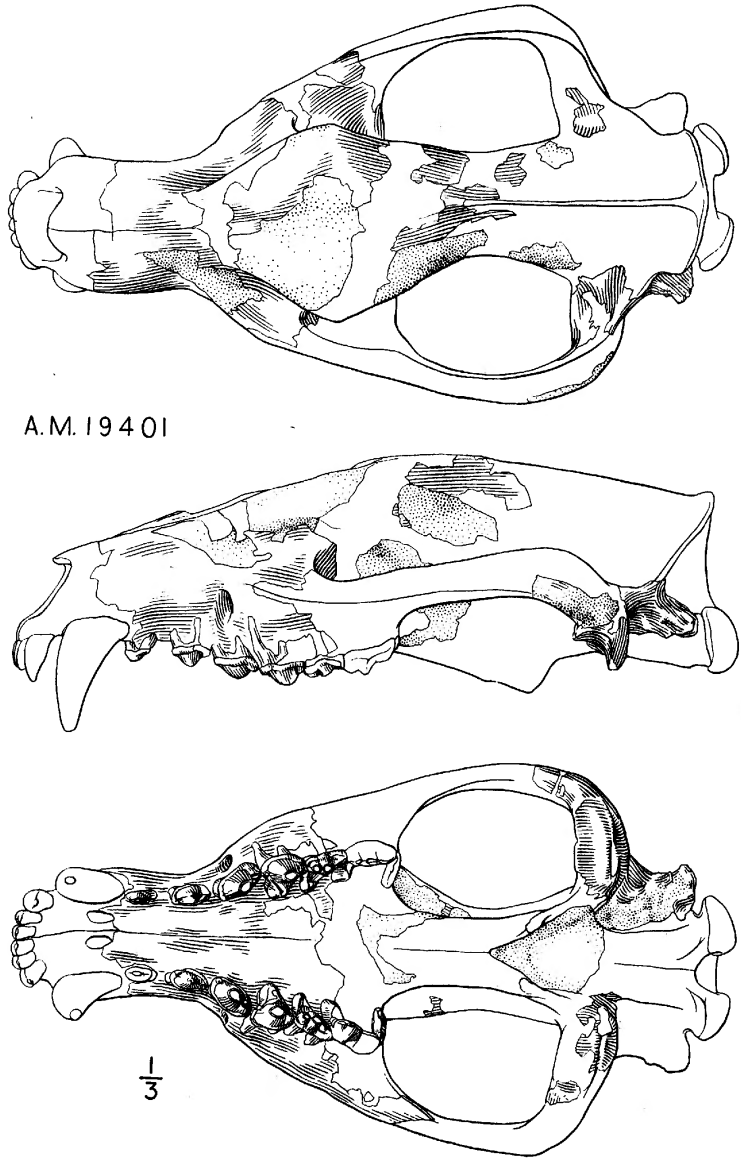


Fig. 1.—*Dissopsalis carnifex* Pilgrim. Amer. Mus. No. 19401. Skull; dorsal view above, lateral view in the middle and ventral view below. One-third natural size.

The dotted areas represent matrix, which indicates the shape of the bone formerly covering these surfaces.

glenoid region is preserved, showing that the paroccipital process is situated far back, and that it does not project downward very much. The bullae, being cartilaginous, were destroyed at the time of fossilization.

THE DENTITION.—

Although the canines are missing, the skull fragment gives some slight indication of their probable size. That is to say, from the shape of the muzzle in front of the first premolar it would appear that the canines were rather strong and heavy.

The presence of the first premolar in the American Museum skull settles a point on which Pilgrim was doubtful, for this tooth was lacking in all of his material. It is a small tooth, elongated antero-posteriorly, with a single cone composing the crown, with slight cingula on the postero-internal and external surfaces, and with an incipient heel behind. It was seemingly almost in contact with the canine. A short diastema separates the second premolar from its predecessor. The second premolar which is larger than the tooth anterior to it, is surrounded by a cingulum; it consists of a large conical cusp, followed by a trenchant heel. The third premolar is relatively long, and in form is much like the preceding tooth. It is surrounded by a cingulum, which expands on the antero-internal corner to form a low cusp. The bulk of the tooth is composed of a large, conical and backwardly directed cusp, followed by a trenchant heel. The last premolar is quite different from the anterior teeth, for it possesses an extremely large and heavy internal protocone, which is of such size that it causes the transverse diameter of the tooth to equal, or even to slightly exceed, the antero-posterior measurement. The outer moiety of the tooth is similar to P^3.

The first molar is perfectly preserved in the skull, and it supplies more accurate information than hitherto known concerning this tooth. The protocone is considerably smaller than Pilgrim figured it,[1] and is connected to the outer portion of the tooth by two ridges, which terminate in two low cusps, the paraconule and metaconule. The paracone and metacone are distinct, but rather closely appressed, and there is a metastyle shear. An external cingulum is present.

The second molar, the principal upper carnassial tooth, is essentially an accentuation of the preceding tooth. The protocone is similar to that of M^1, the paracone is reduced, while the metacone is enlarged and the metastyle shear is elongated. In both M^1 and M^2 the outer cusps are

[1]Pilgrim, G. E. 1914. op. cit., pl. 29, fig. 1.

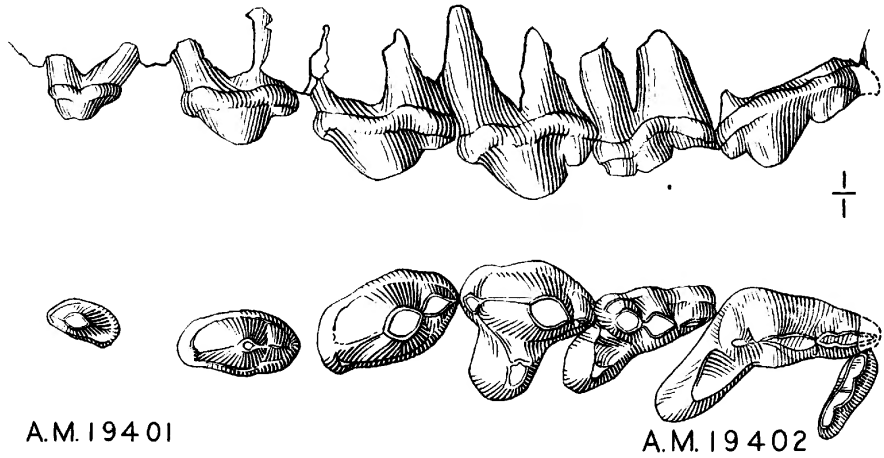


Fig. 2.—*Dissopsalis carnifex* Pilgrim. Amer. Mus. 19401. Right upper premolar and molar teeth. M^2 and M^3 drawn from Amer. Mus. 19402. Lateral view above, and crown view below. Natural size.

elevated above the protocone. The third molar, as seen in A. M. 19402, is a small tooth, considerably smaller than Pilgrim supposed from the fragments he studied. It is a shearing blade, set transversely to the axes of the carnassial blades.

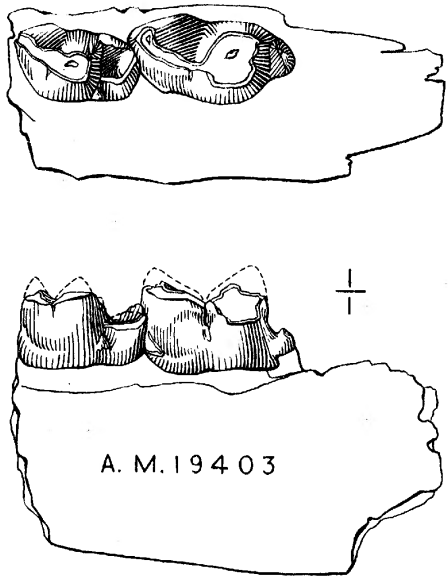


Fig. 3.—*Dissopsalis carnifex* Pilgrim. Amer. Mus. 19403. Left lower second and third molars. Crown view above, and lateral view below. Natural size.

In the mandible, the last premolar, as shown by Pilgrim, consists of a large conical cusp, probably the protoconid, followed by a trenchant heel. The first molar has a strong trigonid, consisting of the protoconid, paraconid and metaconid, and a basined talonid, of which the rim is formed by the hypoconid and entoconid. In the second molar the trigonid is high; the talonid is basin-shaped and relatively smaller than in M_1. In the last molar the trigonid has developed into a large protoconid-paraconid shearing blade, and the talonid has been reduced to a small peg.

TABLE OF MEASUREMENTS

Amer. Mus. 19401						
P^1	Anteroposterior diameter		9 mm.	Transverse diameter		4.5 mm.
P^2	"	"	14.5	"	"	8
P^3	"	"	18.5	"	"	10.5
P^4	"	"	17	"	"	17.5
M^1	"	"	21	"	"	14
Amer. Mus. 19402						
M^2	"	"	23	"	"	13e
M^3	"	"	4	"	"	10
Amer. Mus. 19403						
M_2	"	"	20e	"	'	8.5
M_3	"	"	20.5	"	"	9.5

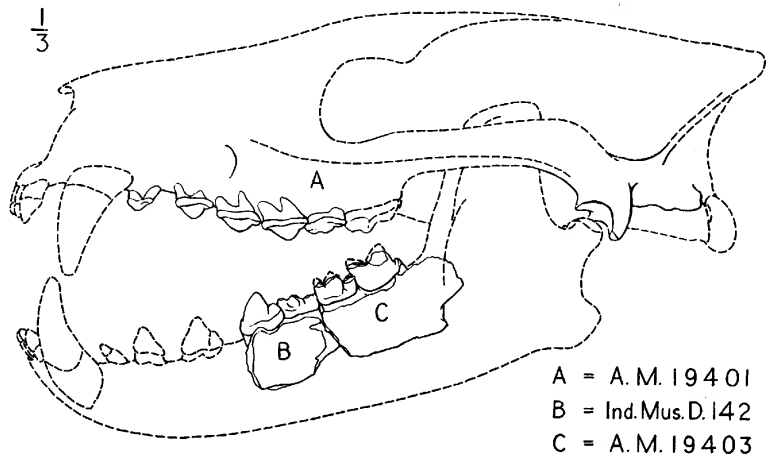


Fig.4.—*Dissopsalis carnifex* Pilgrim. Restoration of skull and mandible, drawn from Amer. Mus. 19401, 19403, and Indian Museum D 142. Lateral view, one-third natural size.

The actual bone and tooth surfaces in place are represented by solid lines. The restored portions, drawn either from crushed bone or matrix, or from hypothetical inferences gained by a study of related genera, are indicated by dotted lines. This figure should be compared with figure 1, to see which portions of the skull were restored from bone and matrix, and which from hypothetical considerations.

AFFINITIES

Dissopsalis, the last known survivor of the creodont line, is peculiarly primitive for such a long-persisting animal. Perhaps its very lack of specialization was a factor in enabling it to live until so late a date. Pilgrim has shown that *Dissopsalis* is clearly derivable from *Sinopa*, and

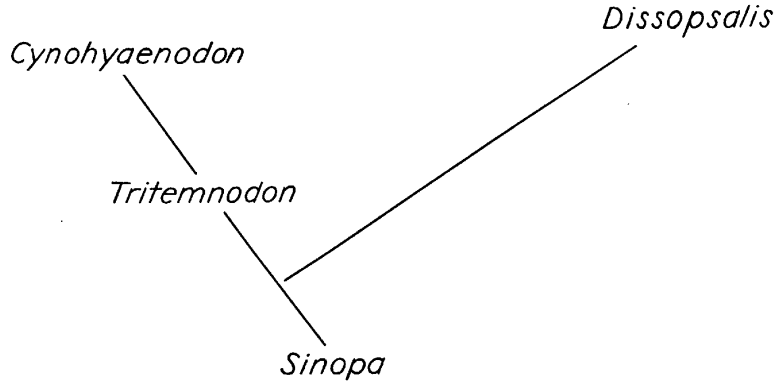
e—estimated measurement.

I think he is essentially correct in regarding the Siwalik genus as an independent phylogenetic line, closely related to *Cynohyaenodon* and *Quercytherium* of Europe.[1]

Considering the skull of *Dissopsalis*, it would seem to have retained the primitive slender shape typical of the early hyænodonts, rather than to have taken on the robustness characteristic of the later genera.

In its dentition, *Dissopsalis* presents a curious mingling of primitive heritage characters and progressive habitus developments. A significant primitive feature in the upper molars is to be found in the relatively wide separation of the paracone and metacone, which presents a decided contrast to the condition in the advanced forms, where these cusps are closely appressed or fused. In addition, the *Dissopsalis* molars are primitive by virtue of the retention of a large protocone. Then again, the lower molars of *Dissopsalis* are primitive in that the trigonids are relatively low, while the talonids, except for that of the third molar, are comparatively large. Considering the advanced characters in the molar teeth of this genus, we see that the carnassial teeth have fairly well developed shearing blades which are disposed along fore and aft axes, causing the teeth to lose their original and primitive triangular outline. In addition to these progressive characters in the anterior molars, there may be mentioned the reduction in size of the last upper molar, and of the trigonid of the last lower molar.

Therefore, considering the mingling of primitive and advanced characters in the teeth of *Dissopsalis*, it would seem logical to suppose that this genus is actually representative of a separate phylogenetic line, having its origin in *Sinopa*.



[1]Pilgrim, G. E. 1914. op. cit., p. 276–7.